

On Mimicry in Butterflies of the Genus *Hypolimnas*.

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[Read 7th November, 1895.]

(PLATES XV.—XVII.)

AFTER studying and thinking over the general theory of Protective Mimicry as described in the works of Bates *, Wallace †, Trimen ‡, Fritz Müller §, Meldola ||, Poulton ¶, and others, it occurred to me that the subject would be advanced by the special study of a small group of wide-spread mimetic species throughout the different countries included in its range.

The *Bolina* group of the nymphalid genus *Hypolimnas* or *Diadema* contains, according to systematists, a number of species. When, however, we look at the group from a biological point of view, we find that all these can be merged in two distinct species—*Hypolimnas misippus* (Linn.) and *Hypolimnas bolina* (Linn.). These I selected for my purpose.

It is first of all necessary to gain a conception of the appearance presented by these species before the mimetic form was assumed. This we find to be still retained by the male of *H. misippus*, which is invariably non-mimetic, and that of *H. bolina*, which is non-mimetic in India and in certain other localities which will be mentioned further on. Occasionally the females also revert to the ancestral pattern and resemble the black males. The non-mimetic males are very similar in appearance, while their mimetic females differ widely. A comparison shows that the male of *H. misippus* is smaller than *H. bolina*, and that the large whitish spot on the upperside of each wing is larger, rounder, and bears very little trace of the blue colour which is so conspicuous in *H. bolina*; while the underside has a reddish hue not present in the latter. On the wing, the male of *H. misippus* is a far more active insect; it is a most pugnacious butterfly, perching on the tops of bushes and darting forward to attack any other butterfly that may fly past; but I have found that when crippled and put at liberty

* Trans. Linn. Soc. xxiii. p. 495.

† Ibid. xxv. p. 19.

‡ Ibid. xxvi. p. 497.

§ Proc. Ent. Soc. Lond. 1879, p. 20.

|| Ann. & Mag. Nat. Hist., Dec. 1882.

¶ Proc. Zool. Soc., March 1887.

it speedily falls a prey to the first bird that sees it. In consequence of these fighting propensities the wings often become battered and torn, although apparently without greatly diminishing the activity of the insect. I have removed half the total wing-surface on one side with a pair of scissors, but the powers of flight did not seem to be much impaired. On two occasions, on Cumballa Hill in Bombay, I entirely removed both wings from one side and placed the insect in an exposed situation. On the first occasion one was eaten by a crow, and on the second by a *Mina*; and in neither case did the birds manifest any hesitation in attacking the butterfly. It is fair to conclude from these observations that the species is not distasteful.

The female of *H. misippus* however, except as a very rare variety which resembles the male in appearance, always mimics the commonest of all the *Danainæ*, i. e. *Danaïs chrysippus* (Linn.), Pl. XV. fig. 2, which is common all over India, Burma, Ceylon, the Malay Archipelago, Madagascar, Aden, and the West, South, and South-eastern coasts of Africa, but apparently not the interior: in all these localities *Hypolimnas misippus* also exists, the female being of the *Danaïs* colour and pattern (see fig. 1); and where *Danaïs chrysippus* does not exist, *Hypolimnas misippus* is not to be found*.

In Africa *D. chrysippus* is of a dull bronzy red, and not nearly so brightly coloured as it is in Asia; and similarly the females of *H. misippus* in Africa are dull bronzy red, whereas in Asia they are brightly coloured.

In Africa and at Aden there are several forms of *Danaïs chrysippus*—some without the white-banded black apical patch to the fore wings (*D. dorippus*, Klug), fig. 4; some possessing this marking, but characterized by white hind wings (*D. alcippus*, Cram.), fig. 6; and also others with the *D. dorippus* pattern and white hind wings. All these forms are mimicked in their several localities by the females of *H. misippus*: compare fig. 4 with 3, and 6 with 5.

In India the form of female *Hypolimnas* which mimics *Danaïs dorippus* (without the black and white apical patch) is also

* Distant, in Rhop. Malay. p. 168, states:—"This species (*H. misippus*) in its female sex affords one of the best and strongest examples of 'mimicry,' it being a true and startling mimic of *Danaïs chrysippus*, a protected species which is found with it in its different habitats, excluding America, where, however, it is evidently an introduced species."

found: it is not nearly so frequently met with as the mimic of the true *D. chrysippus*, but it is not uncommon, being occasionally found nearly all over India. So far as I am aware, the particular form of the *chrysippus* group (*D. dorippus*, Klug) which it mimics had never been recorded from India; and it struck me as extraordinary that we should find in India the mimic of a protected insect which is not an inhabitant of the same countries. The two forms of protected insects are exactly alike on the wing; and as no one collects the common *D. chrysippus*, I could not but believe that the explanation of the apparent anomaly lay in the fact that *D. dorippus* had been overlooked. In order to test this conclusion, I engaged two native collectors for three months to catch nothing but *D. chrysippus*. I thus obtained, as may be imagined, many thousands, and the experiment was most successful, because amongst them I obtained no fewer than twelve individuals of *D. dorippus*. This was in Bombay in 1883; in the following year, when in Karachi, in Sind, I obtained three examples, and Major Yerbury sent me two from the Punjab. From the circumstance that the *dorippus* form of *Hypolimnas misippus* is not uncommon, while the same form of the *Danais* is comparatively rare, I am inclined to believe that the latter is dying out in India, and is being replaced by *D. chrysippus*, and that the mimetic form has actually outlasted the form it has mimicked. It must be remembered, however, that the resemblance of the *dorippus* form of the *Hypolimnas* to the typical *Danais chrysippus* is sufficiently striking to afford considerable protection; and hence natural selection would only cause a very gradual return to the other form, on which we must believe that still greater immunity is conferred.

In the species *H. bolina* (Linn.) as we find it in Asia, the female only is mimetic, the male in all localities being of the normal form; in India the female universally mimics the common protected butterfly *Euplœa core* of Cramer. The typical *E. core* does not range very far south, one or two have been taken in Mergui, but there is no record of its more southern extension, its place being taken by other common black *Euplœas* of somewhat similar pattern. We find accordingly that *H. bolina* varies so as to resemble all the common *Euplœas* of the different islands of the Malay Archipelago.

The Amboina form of *H. bolina* mimics *E. climena*, Cram. In Sumatra it is known as *Hypolimnas anomala*, and mimics

Isamia (Euplœa) singapura, Moore. In Ké Island, under the name of *Hypolimnas polymena* (Pl. XVI. fig. 2), they mimic *Euplœas* with broad whitish borders to the uppersides of the wings (Pl. XVI. fig. 1), a form of pattern common among the *Euplœas* in this island. I have no fewer than three well-defined subgenera of *Euplœas* with such broad white borders from Ké Island—*Calliplœa Hopfferi*, Felder (fig. 1), *Chirosa eurypon*, Hewitson, and *Hirdagra fraterna*, Felder, all possessing well-marked sexual subgeneric distinctive characters.

From the Solomon group I have examples from two islands: in Maleita Island both sexes are mimetic, the male (fig. 3) and female (fig. 5) of the *Hypolimnas* known as *Hypolimnas scopas* respectively mimicking the corresponding sexes of *Euplœa pyrgion* (male fig. 4, female fig. 6). This is a very interesting example, because the differences between the two sexes are fairly distinctive and constant. In another island of this group both sexes (Pl. XVII. fig. 1) mimic *Euplœa polymena* (fig. 2). In this case no local name, so far as I know, has yet been bestowed upon the *Hypolimnas*.

In the Fijis the male of the local unnamed form of *H. bolina* is normal in appearance, but the females occur in many varieties, and seem to exhibit a regular gradation from an appearance like that of the normal male to brown, and from brown to yellow and white, as if the mimetic resemblance was still in a state of transition. In Messrs. Godman and Salvin's fine collection there are upwards of sixty varieties of the female, and on the table are upwards of seventy examples from my own collection showing many varieties; and this is the only instance I have found of any local variation in the mimetic forms of this species. The only two *Euplœas* I have seen from the Fijis are *E. Whitmei* (Butler) and *E. margoensis* (Butler), the first from Lifu Island and the second from Margo. These are dark *Euplœas* and resemble the dark forms of the female *bolina*. But we know very little about the Fijian Lepidoptera, and there may very well be other *Euplœas* corresponding to other forms of the female *Hypolimnas* inhabiting the same locality.

In many of the Southern Islands *H. bolina* in its typical form is found with females mimicking red forms of *Danais*; I have examples from Celebes, Ké Island, Alu, New Britain, and also from North Australia. The Celebes female called *H. nerina*, Felder, is a fair mimic of *Danais chionippe*, Hübn., also found in the same locality; there are probably other similar forms of

red *Danais* in these islands. The mimic is here much larger than the mimicked. This is the only case I know of, in which this species of *Hypolimnas* mimics a red insect and thus gains itself a considerable patch of this colour.

Next we turn to Africa, and we invariably find that both sexes of what we may fairly call the African forms of *Hypolimnas bolina* mimic various species of *Danainæ*, the normal form of the male having entirely disappeared. Hence, from the systematist's point of view, the specific characters having been lost in both sexes, they bear as many specific names as there are local forms mimicking the accompanying species of *Danais*.

In quest of these mimetic forms, I searched through Mr. Crowley's magnificent collection of African butterflies at Croydon, where I found very many examples, from which I selected three. In every locality where the forms occur, the mimicry seems to be remarkably perfect, but there are local peculiarities in the patterns of both mimic and mimicked in many places. The localities are as widely separated as Natal in the South-east, and the Cameroons in the West of Africa.

From Natal, I have obtained *Hypolimnas marginalis* (Pl. XVII. fig. 3), which mimics *Amauris dominicanus* (fig. 4). From Grahamstown, *H. mina* mimicking *A. echeria*; from the Cameroons, *H. dubia* (fig. 5) mimicking *A. egialea* (fig. 6).

CONCLUSIONS.

Having thus brought together all the facts I have come across and those which have been previously published, it remains to ascertain their bearing upon the theory of mimicry, for this theory has never been subjected to the evidence derived from the systematic study of a small group of wide-ranging, mimetic insects, carefully traced through all the localities included in their range. This has, however, been done for the *Papilio merope* group, so admirably worked out by Roland Trimen (Trans. Linn. Soc. xxvi. p. 497, and South-African Butterflies, vol. iii. 1889, pp. 243-55), but the total range of these butterflies is far more limited and the number of different forms much smaller than is the case with the *Hypolimnas* group.

Bearing upon general Theory of Mimicry.

In the first place, we find the strongest support to the general theory of mimicry as originally suggested by H. W. Bates. The

varied changes which occur are explained by this theory, and by no other yet propounded. When we trace *Hypolimnias bolina* from India into Amboina, Sumatra, Ké Island, two islands of the Solomon group, Fiji, Celebes, and various part of Africa, we meet with a different form in each locality, a form which from the biological standpoint may be called the *Hypolimnias bolina* of the locality. That local changes should occur may be intelligible in many theories, but that they should invariably be in the direction of a superficial resemblance to one butterfly (or in some cases two or more distantly related butterflies) out of the numerous and varied Rhopalocerous fauna of each locality, and that one a specially defended species, well known and avoided by insect-eating animals, is only to be explained by the theory of mimicry,—by the advantages conferred by relatively greater resemblance having acted as a selective test during all the stages of development. The theory of mimicry has received much support by the investigations which have been carried on since Bates propounded it in 1862, but I believe that no evidence is so complete and convincing as that supplied by the genus *Hypolimnias*.

Bearing upon the special liability of female to mimetic resemblances.

The facts also bear in an interesting manner upon the details as well as upon the general theory. Thus the observation that females are more liable to be defended by mimicry than males, and its explanation (suggested by A. R. Wallace), as due to their "slower flight when laden with eggs, and their exposure to attack while in the act of depositing their eggs upon the leaves," receives further support and confirmation. Among the numerous forms of both the *misippus* and *bolina* group, we meet with no case in which the male is mimetic while the female is non-mimetic: the male of *misippus* is peculiarly active on the wing, and being able to defend itself in this way, is never mimetic; the male of the less active *bolina* affords a beautiful transition from the condition met with in *misippus* to a mimicry as complete as that of the female. In this respect the group is far more interesting than that of *P. merope*, in which the males are never mimetic.

The ancestral non-mimetic form from which the mimetic varieties have been derived: various phases of development of mimicry.

The ancestral form of both groups is preserved in the closely similar non-mimetic males, and the rare cases of reversion to the same type exhibited by the females. But the beautiful evidence supplied by the existence of the ancestral non-mimetic form of both sexes in certain islands is wanting here, although so well seen in the *merope* group.

The most ancestral form described in this paper is probably the Fijian *bolina*, in which the females exhibit a transition from non-mimetic to mimetic forms; then would follow the Indian *bolina*, in which the female is not a very perfect mimic of *Euplœa core*, and still retains traces of the blue spots so characteristic of the non-mimetic males, culminating in the Celebes form, in which the mimicry of the female is fairly complete and has entailed a more marked divergence from the normal type than any other form in this group: at this stage *misippus* must be placed, with its non-mimetic male and females with extremely perfect and detailed mimicry. We finally reach the climax of change in those island forms of *bolina* in which the males also are mimetic, and in Africa, where no more ancestral phase is at present known.

Bearing upon mimetic resemblance to different species in one locality.

The well-known mimetic resemblance to two or more very differently coloured species of distasteful insects in the same locality is not well exemplified, although it appears probable that some varieties of the females from Fiji bear this interpretation, which may also in part explain the occurrence of all three varieties of the female *misippus* at Aden, where the three corresponding forms of *Danais* are also found (viz. *chrysippus*, *alcippus*, and *dorippus*). But here, too, we meet with nothing that approaches the condition of some species of the *merope* group of the S.-African *Papilio cenea* for example, in which four forms of the female respectively mimic such differently coloured species as *Danais chrysippus*, *Amauris dominicanus*, and two varieties of *Amauris echeria*, thus widening the area of possible mistake so far that the mimetic species can become comparatively numerous without the risk of extermination.

*Different conditions under which mimicry may appear :
attempted explanation.*

Finally our facts have an instructive bearing upon the very different conditions under which mimicry may appear in the most closely related species. It seems clear that we have to do with two species which are unable to exist without this deceptive resemblance to some specially protected form, either in both sexes or in the one which is chiefly exposed to attack. Wherever we find these butterflies, whatever changes they may undergo, the resemblance which enables them to live upon the reputation of some local distasteful species is maintained. Mimicry being equally necessary to both *misippus* and *bolina* in order to ward off extermination, we nevertheless find that it pursued an utterly different course in these two species. *Hypolimnas misippus* has attached itself to a single well-known, conspicuous, wide-ranging species of distasteful butterfly, resembling it with great fidelity, and following it through the details of even minor changes. In order to achieve this result, it has been compelled to depart very widely from the ancestral form—even more so than is the case with any of the *bolina* group. But this extreme variation in one direction appears to have deprived it of the power of developing variations in other directions; so that its existence and range seem to depend upon the existence and range of a single butterfly, *Danais chrysippus* and its varieties. In *Hypolimnas bolina*, on the other hand, we meet with much greater elasticity: its range is almost unlimited as regards the conditions imposed by mimicry, for it can vary in each locality into the semblance of some local species.

How is this wide divergence to be explained? Many biologists would be inclined to lay stress on the amount and kind of individual variation which has been at the disposal of the selective process during the development of the mimetic resemblance; and it is certain that the results must have been largely influenced by this. It is noteworthy that *bolina* includes forms which are both older and younger than those of *misippus*, the latter representing but a single one out of the many phases of departure from the ancestral type represented by the former. It may be that this comparatively narrow limitation of *misippus* is merely due to the exclusive predominance of a single specially advantageous resemblance, *Danais chrysippus* being so abundant and well-known in the localities where it occurs, and its distribution affording scope for a wide range. Or variation may have carried

misippus in this direction from the very first, and sufficient protection being thus conferred there would be no tendency towards the production of other forms. In either case we must look upon the selective process as chiefly responsible for the result. It is impossible to deny abundant powers of variation to *misippus*, when we remember its faithful resemblance to the special changes undergone by *D. chrysippus*. But variation being under the guidance of selection in one direction only, has produced nothing in any other direction. It is easy to imagine conditions under which *H. bolina* might become equally restricted. If *Euplœa core* had the distribution of *Danaïs chrysippus*, it is probable that no other mimetic variety would have been produced. Or if *Danaïs chionippe* of Celebes had the range and abundance of *D. chrysippus*, it is probable that the superior advantages attending the resemblance to it might cause the ultimate predominance of this one out of the many mimetic forms of *H. bolina*.

If, then, we are right in believing that the results are determined by the range and abundance of the mimicked form, because this, through selection, determines the number and kind of the mimicking varieties, it is clear that selection rather than unguided variation is the essential cause of the phenomena, always assuming the necessary amount of variation for selection to act upon.

The fact that selection follows, where possible, the path of least resistance as regards variation, is well seen in *H. bolina*. Not one of its many mimetic forms departs so widely from the ancestral appearance as those of *misippus*, and for the production of most of them comparatively small changes are necessary. In India and Malaya, with a single exception, various dark-coloured *Euplœas* are mimicked. The interesting exception of the *chionippe* form proves that much greater divergence is possible, and that the path provided by the easiest and most probable variation is only followed when it is advantageous. When we pass into Africa, we find that the place of the genus *Euplœa* is taken by the *Danaïs* genus *Amauris*, and dark-coloured butterflies of this specially protected genus have afforded ready models for mimicry, so that here too the necessary conditions have been met by less divergence than has been necessary for *H. misippus*.

My thanks are due to Messrs. Godman, Salvin, and Crowley for examples of various mimetic forms, and especially to Professor Poulton for much kindly assistance in deducing the above conclusions.

EXPLANATION OF THE PLATES.

PLATE XV.

- Figs. 1, 3, 5. *Hypolimnas misippus*, ♀ (3 forms).
 Fig. 2. *Danaïs chrysippus*.
 4. " *dorippus*.
 6. " *alcippus*.

PLATE XVI.

- Fig. 1. *Euplœa Hopfferi*. Fig. 2. *Hypolimnas polymena*.
 4. " *pyrgion*, ♂. 3. " *scopas*, ♂.
 6. " " ♀. 5. " " ♀.

PLATE XVII.

- Fig. 2. *Euplœa polymena*. Fig. 1. *Hypolimnas*, sp.
 4. *Amauris dominicanus*. 3. " *marginalis*.
 6. " *egialea*. 5. " *dubia*.

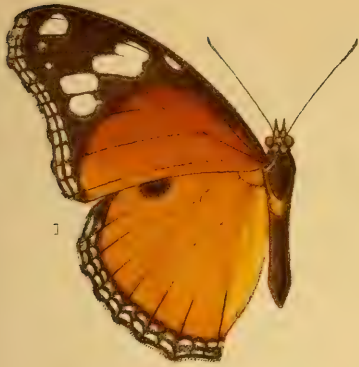
An Account of the Butterflies of the Genus *Charaxes* in the Collection of the British Museum. By ARTHUR G. BUTLER, Ph.D., &c., Senior Assistant-Keeper, Zoological Department.

[Read 7th November, 1895.]

ONE of the first genera which I ever studied, and the first which I monographed, was the genus *Charaxes*, a paper on which I published in 1865 in the 'Proceedings of the Zoological Society,' in which I recorded sixty-eight species (two of which, however, were noted as doubtful and were subsequently suppressed): the present paper enumerates no fewer than one hundred and fifty-nine.

I have followed Prof. Aurivillius in uniting *Palla* to *Charaxes*: if kept separate, it would have to be broken up into several genera, and *Charaxes* itself would in like manner have to be subdivided; this, indeed, has been done for the Indian species by Mr. Moore; but apart from outline of wing I have been unable to discover any constant structural characters on which to base these genera. That wing-outline in *Charaxes* is not of generic importance seems clear, from the fact that (i.) in many of the species it differs to an extraordinary degree in the sexes; (ii.) the most nearly related species (as, for instance, *C. Balfouri* and *C. varanes*) differ in this respect as much as any of the proposed new genera; and, lastly, (iii.) it is not uniform, even when apparently so to a casual observer, the shortening or absence of the hind-wing tails occurring abruptly in a single species in the middle of a group.

When I last arranged *Charaxes*, about the year 1892, our series occupied a single cabinet of 20 drawers; last year, however, MESSRS. Salvin and Godman (with their usual liberality)



1



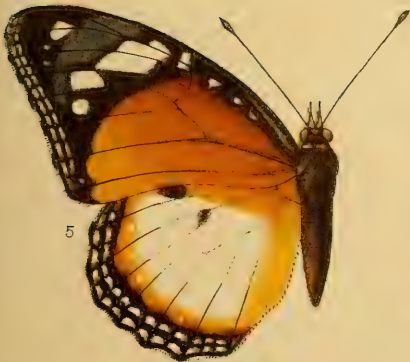
2



3



4



5



E.C. Knight del et lith.

West, Newman chromo.

1. 3. 5. HYPOLIMNYS MISIPPUS, ♀ (3 FORMS) 2. DANAIS CHRYSIPPUS.
 4. DANAIS DORIPPUS. 6. DANAIS ALCIPPUS.



1



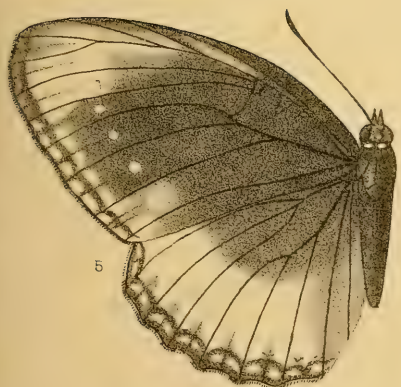
2



3



4



5



6

E.C.Knight del. et lith.

West, Newman imp.

1. EUPLOEA HOPFFERI. 2. HYPOLIMNAS POLYMENA.
3. 5. HYPOLIMNAS SCOPAS ♂. ♀. 4. 6. EUPLOEA PYRGION. ♂. ♀.



E.C.Knight del. et lith.

West, Newman imp.

1. HYPOLIMNAS SP. 3. H. MARGINALIS. 5. H. DUBIA.
2. EUPLCEA POLYMENA. 4. AMAURIS. DOMINICANUS. 6. A. EGIALE. A.